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The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis

A. W. TRITES and C. P. DONNELLY
Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, B.C., Canada V6T 1Z4

ABSTRACT

1. The decline of Steller sea lions *Eumetopias jubatus* in the Gulf of Alaska and Aleutian Islands between the late 1970s and 1990s may have been related to reduced availability of suitable prey. Many studies have shown that pinnipeds and other mammals suffering from nutritional stress typically exhibit reduced body size, reduced productivity, high mortality of pups and juveniles, altered blood chemistry and specific behavioural modifications.

2. Morphometric measurements of Steller sea lions through the 1970s and 1980s in Alaska indicate reduced body size. Reduced numbers of pups born and an apparent increase in juvenile mortality rates also appear to be nutritionally based. Blood chemistry analyses have further shown that Steller sea lions in the Gulf of Alaska and Aleutian Islands area exhibited signs of an acute phase reaction, or immune reaction, in response to unidentified physical and/or environmental stress. Behavioural studies during the 1990s have not noted any changes that are indicative of an overall shortage in the quantity of prey available to lactating female sea lions.

3. The data collected in Alaska are consistent with the hypothesis that Steller sea lions in the declining regions were nutritionally compromised because of the relative quality of prey available to them (chronic nutritional stress), rather than because of the overall quantity of fish *per se* (acute nutritional stress). This is further supported by captive studies that indicate the overall quality of prey that has been available to Steller sea lions in the declining population could compromise the health of Steller sea lions and hinder their recovery.

Keywords: northern sea lion, nutrition, pinnipeds, population decline

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Correspondence: A. W. Trites, Email: trites@zoology.ubc.ca

INTRODUCTION

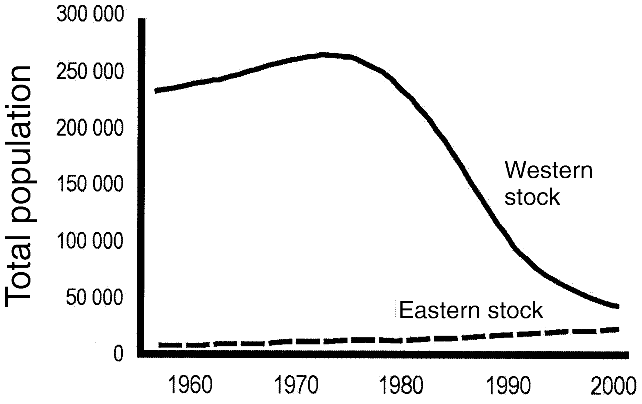
Over the past five decades, significant changes have occurred in the abundances of seals and sea lions around the world. Examples in the southern hemisphere are increases of Antarctic fur seals *Arctocephalus gazella* and declines of Southern elephant seals *Mirounga leonina* (Trillmich, 1986; Boyd, Arnbom & Fedak, 1994a; Knox, 1994; Guinet, Jouventin & Weimerskirch, 1999) – while in the northern hemisphere, Steller sea lions *Eumetopias jubatus*, northern fur seals *Callorhinus ursinus* and harbour seals *Phoca vitulina richardsi* decreased in the Bering Sea and Gulf of Alaska, and increased between Southeast Alaska and California (Bigg, 1988; Olesiuk, Bigg & Ellis, 1990; Pitcher, 1990; Trites, 1992; Ferrero *et al.*, 2000; Gerber & Hilborn, 2001). Such changes are potentially caused by the effects of predation, disease and nutrition on reproduction and mortality, but are difficult to demonstrate convincingly.

The Steller sea lion ranges from northern California, through Alaska, to Russia and northern Japan, and has been the subject of intensive studies to determine what caused its dramatic decline (Fig. 1). The decline is believed to have begun in the eastern Aleutian Islands, and spread throughout the Aleutian Islands and the Gulf of Alaska by the late 1970s (Braham, Everitt & Rugh, 1980; Trites & Larkin, 1996). The exception to this trend was in Oregon, British Columbia and Southeast Alaska where sea lion numbers increased (Merrick, Loughlin & Calkins, 1987; Bigg, 1988; Trites & Larkin, 1996; Calkins, McAllister & Pitcher, 1999).

Steller sea lions declined rapidly in the Gulf of Alaska and Aleutian Islands through the 1980s, and at a slower rate during the 1990s (Fig. 1). Some suspect this change in rate of decline reflects a change in a factor or suite of factors that has ultimately driven the population decline (NMFS, 2001). However, it is equally possible that the ultimate cause has remained the same and that the slowing of the decline reflects a population approaching a new, but lower, carrying capacity.

The leading hypothesis to explain the rapid decline of Steller sea lions is that the population in the Gulf of Alaska and Aleutian Islands was nutritionally stressed because of a reduction in overall prey abundance, or because of a change in the relative abundance of different types and quality of prey available. However, it has been difficult to test or evaluate this hypothesis. Sample sizes for most data sets have been small because of the inherent challenges in studying

Fig. 1. Estimated numbers of Steller sea lions (all ages) in Alaska from 1956 to 2000 (from Trites & Larkin, 1996; A.W. Trites, unpublished data).



Steller sea lions in the wild. Most data sets were also not collected to test the nutritional stress hypothesis, and there is also some confusion over what sorts of changes should be observed if Steller sea lions are, or were, nutritionally stressed.

The following reviews the evidence for nutritional stress in Steller sea lions. One of the components of this hypothesis that we examine is the role that changes in quality rather than quantity of prey may have played in the population decline. We also provide a brief overview of how mammals in general respond to nutritional deprivations. Our synthesis sheds light on the forces that have driven the Steller sea lion decline and may be instructive to others attempting to decipher the role that nutritional changes may play in the dynamics of other species of marine mammals.

PINNIPEDS AND NUTRITIONAL STRESS

Nutritional stress is a negative physiological and/or behavioural state resulting from sub-optimal quantity or quality of food available to an animal. Effects of nutritional stress (and responses to nutritional stress) in terrestrial and marine mammals include reduced body size, reduced birth rates, increased neonate mortality, increased juvenile mortality, behavioural modifications (e.g. longer foraging bouts), and changes in blood chemistry and body composition.

Reduced body size

Sub-optimal consumption can stunt or reduce body size in animals. Humans with eating disorders that result in drastic food reductions suffer low body weights, extremely low body fat percentages and emaciation (Bulik *et al.*, 1999; Mathiak *et al.*, 1999). Laboratory rats with restricted food intakes will attain lower weights because of slower growth rates and less accumulated body fat (Peckham, Entenman & Carroll, 1962; McShane & Wise, 1996; Nieuwenhuizen *et al.*, 1999).

El Niño events in the mid- and south Pacific Ocean provide opportunities for determining the effects of a known nutritional stress on marine mammals. During the 1983 El Niño, a combination of increased sea surface temperatures, less upwelling and a depressed thermocline reduced available nutrients to organisms in the euphotic zone (Majluf, 1991). This acute event led to a collapse of primary productivity (phytoplankton), which in turn reduced secondary productivity and caused subsequent shortages of prey for many marine mammals. In Peru, this cascade of events decreased the abundance of anchovies *Engraulis ringens*, which in turn reduced the growth of South American fur seal pups *Arctocephalus australis* compared to three other years when anchovy stocks were plentiful (Majluf, 1991). Southern sea lions *Otaria byronia* in Peru also appeared emaciated during this El Niño event, although measurements were not taken (Majluf, 1991). In the Galapagos Islands, newborn fur seals *Arctocephalus galapagoensis* were 10% lighter than those born during non-El Niño years, and several emaciated yearlings were sighted and subsequently disappeared (Trillmich & Limberger, 1985).

In general, El Niño events are associated with an absence of prey that may elicit strong density–dependent responses over a relatively short period of time (1–3 years). Regime shifts on the other hand may favour the survival of certain suites of prey species over others, thereby inadvertently altering the relative quality of prey that pinnipeds consume (Benson & Trites, 2002). Thus, compared to El Niño events, regime shifts may evoke subtle density-dependent changes over longer time frames (10–30 years).

On a short term, animals faced with reduced quantity or quality of food will lose body weight unless they compensate by sufficiently reducing their activity or metabolism (Øritsland & Markussen, 1990; Westerterp *et al.*, 1995). This has been shown for captive Steller sea lions that lost an average of 0.6 kg/day over 3 weeks when their energy intake was reduced from approximately 42 to 33 MJ/day (Rosen & Trites, 2000b). Over a longer term, however, a lower nutritional plane could conceivably stunt growth.

Reduced productivity

Reproduction is linked to metabolism by a complex web of hormones and feedback systems (Booth, 1990; Barash *et al.*, 1996; Barb *et al.*, 1998). As nutritional stress becomes acute, animals are less likely to bear young. In humans and other mammals, this is manifested through irregular oestrus or menstrual cycling, prolonged infertility in adolescence, retarded peak fertility and increased occurrence of spontaneous abortions (Frisch, Wyshak & Vincent, 1980; Guinet *et al.*, 1998; Bulik *et al.*, 1999).

Reproduction can be terminated at any point during the reproductive cycle, from ovulation to parturition. However, the critical stage at which this happens appears to differ among species. For example, in humans, nutritional insult results in cessation of ovulation (Frisch *et al.*, 1980). In pinnipeds, the crucial periods seem to be late gestation and the subsequent survival of newborn pups (Trillmich & Limberger, 1985). The frequency of pregnancy in pinniped populations during early gestation is not always reduced, indicating that ovulation and fertilization are more resistant to stress in pinnipeds. Late gestation and lactation pose a significantly larger energetic cost to females as they support rapidly growing foetuses and neonates in addition to their own metabolic requirements (Trites, 1991; Pitcher, Calkins & Pendleton, 1998). When food resources are scarce during this costly stage, reproduction and pup survival appear to be jeopardized.

During the 1983 El Niño, the number of Galapagos fur seals born was only 11% of average levels (Trillmich & Limberger, 1985). Births of Galapagos sea lion pups *Zalophus californianus wollebaeki* also declined during this year of food shortage (to 74% of pre-El Niño levels; Trillmich & Dellinger, 1991). Similarly, northern fur seal pup production decreased by 60% during the 1983 El Niño at San Miguel Island, California (DeLong & Antonelis, 1991). In the southern hemisphere, the length of pregnancy of Antarctic fur seals was longer and the date of birth was later in years associated with reduced prey availability (Boyd, 1996). Fewer Antarctic fur seal pups also appear to be born following a year of food restriction (Lunn & Boyd, 1993) – while in the North Atlantic, higher proportions of grey seals *Halichoerus grypus* failed to give birth following years of low sandeel *Ammodytes dubius* abundance (Pomeroy & Duck, 2000).

From late 1993 to early 1994, an unusual intrusion of warm, poorly oxygenated water along the coast of Namibia resulted in massive reductions in sardines *Sardinella aurita* and anchovies *Engraulis encrasicolus* (Roux, 1997). Over 40 000 aborted foetuses from South African fur seals *Arctocephalus pusillus* were counted at one colony alone (Roux, 1997). A 4-year study found female fur seals that aborted pregnancies were in significantly poorer body condition (as indicated by a low body condition index) than those that maintained pregnancies to parturition (Guinet *et al*., 1998). This study also found a significant positive relationship between body condition and the probability of being pregnant in late gestation. Nutritional stress can thus reduce body size and condition of pinnipeds, which in turn correlates with reduced numbers of births. The extent of such effects appears to be related to the intensity of the nutritional insult.

Birth weights and growth rates

Birth weights may reflect the mother's condition during pregnancy, while growth rates during lactation may be indicative of both the condition of the female and her ability to procure food to produce milk. Abundant prey that led to short foraging trips by pregnant mothers resulted in heavier birth weights in Antarctic fur seals, compared to years when food was less abundant and foraging trips were longer (Lunn, Boyd & Croxall, 1994). In Namibia, a reduction in prey abundance in 1994–95 resulted in the lowest masses of South African fur seal pups ever recorded (Roux, 1997). Similarly, the 1982–83 El Niño event resulted in Galapagos fur seals giving birth to pups on the Galapagos Islands that weighed 9–10% less than expected, and the food shortage continued to affect these pups until they weaned (Trillmich & Limberger, 1985). Extended foraging trips for scarce food meant that pups were left to fast for long periods (4.5 days vs. 1.2 days) and had slower growth rates (Trillmich, 1990). A similar reduction in pup growth was also found in California sea lions *Z. c. californianus* (Ono, Boness & Oftedal, 1987), South African fur seals (Roux, 1997), and Antarctic fur seals (Trillmich, 1990) during periods of food shortages. Thus nutritional stress can reduce birth weights and subsequent growth rates of dependent pups.

Reduced pup survivorship

Trillmich & Limberger (1985) reported that only 67% of Galapagos fur seal pups survived their first month of life and that none were alive after 5 months during the 1983 El Niño in the Galapagos Islands. In contrast, when food was abundant during the non-El Niño years of 1979–81, 95% survived during the first month and 80% survived the first year. The Galapagos sea lion also experienced high pup mortalities during 1983, with only 14% surviving vs. 95% surviving in typical years (Trillmich & Dellinger, 1991). Similar results were reported for South African fur seals in 1994–95 when anomalous oceanographic conditions reduced the abundance of their prey in Namibia (Roux, 1997).

Mothers faced with food shortages are often only able to allocate enough resources to meet their own metabolic needs and are unable to provide sufficient energy to their pups. Thus, young offspring of food-deprived females suffer most dramatically during severe reductions of prey (Trillmich & Limberger, 1985; Trillmich & Dellinger, 1991).

Reduced juvenile survivorship

Juvenile pinnipeds that forage on their own are faced with greater nutrition-related challenges during food shortages than older, more experienced individuals. Adults have the ability to substantially increase the time and distance of their foraging trips, and can execute deeper dives than juveniles. In contrast, juveniles have higher relative energy demands (Boyd, 2002;

Winship, Trites & Rosen, 2002) and are usually inexperienced foragers, and may not be able to increase their foraging effort through behavioural adaptations (Merrick, 1995). They may therefore incur higher rates of mortality than older individuals through starvation or the secondary effects of predation and disease.

The 1983 El Niño was particularly hard on juvenile Galapagos fur seals and Galapagos sea lions. Juvenile sea lion survival was only 20% of normal during this time of extreme food shortage. Seven of nine yearlings appeared to be starving and later disappeared. None of 143 2-year-olds returned to their colonies, and only six of 12 3-year-olds returned – all others were presumed to have starved at sea (Trillmich & Limberger, 1985). Adult female numbers, on the other hand, were only reduced by 27%. These older animals were likely better able to seek out prey during the shortage, thereby buffering the effects of El Niño by modifying their foraging behaviour. Similar observations have been made of emaciated and starved juvenile age classes of South African fur seals in Namibia (Roux, 1997), and of Northern fur seals, northern elephant seals *Mirounga angustirostris* and California sea lions during El Niño events along the coast of California (Mair, 1998; Zagzebski, Phillips & Gulland, 1999).

Unusually large numbers of harp seals *Phoca groenlandica* were caught by gillnet fisheries along the Norwegian coast in 1987 and 1988 (Haug *et al.*, 1991). Most of the entangled seals were juveniles and most were in poor body condition (Øritsland, 1990). The 'invasion' of harp seals is thought to have resulted from a collapse of capelin stocks in the Barents Sea that was caused by fisheries and predation by herring (Nillsen *et al.*, 1998). Few of the harp seal pups born from 1986 to 1988 survived to sexual maturity (Kjelliqwist, Huag & Øritsland, 1995).

Large numbers of emaciated, yearling northern fur seals washed ashore in the late 1940s in Washington and Oregon (Scheffer, 1950). Their deaths were probably because of harsh winter conditions, low fat reserves and their inability to forage effectively in rough seas. Similar observations were not made of adult fur seals, suggesting that juveniles are more vulnerable than adults to changes in prey availability.

Malnourished animals are also more susceptible to disease and parasitism, which can make them more susceptible to predation (Grenfell & Gulland, 1996). Harbour seals, for example, had higher parasite levels among individuals that were in poor condition following years of poor food availability (Thompson, Corpe & Reid, 1998). This in turn may affect haematology.

Blood parameters

Another way that nutritional stress can be detected in marine mammals is through plasma and haematological tests. For example, malnutrition in northern fur seal pups is indicated by viscous blood and dehydration in all tissues (Keyes, 1965). In Amazonian manatees *Trichechus inunguis*, blood glucose, urea and lipid levels are related to paragrass protein and lipid contents, thus indicating the nutritional status of the animal (Colares *et al.*, 2000). In Steller sea lions, blood glucose levels reflect carbohydrate utilization, while non-esterified fatty acids (NEFA) and β-hydroxybutyrate (ketone bodies) reflect fat utilization (Rea *et al.*, 1998). Levels of NEFA and ketone bodies are elevated when an animal fasts, and drop as an animal enters Phase III starvation (Castellini *et al.*, 1993; Rea, Rosen & Trites, 2000). Phase III starvation is defined as the last stage of starvation when both glucose and fat stores are depleted and an animal begins to use its protein stores (e.g. muscles) as an energy source (Cherel *et al.*, 1992). Elevated blood urea nitrogen (BUN) is a measurable sign of this third phase.

In northern elephant seals, fasting has been shown to increase blood ketone (β-hydroxybutyrate) levels (Castellini & Costa, 1990). Blood chemistry analyses of 10 wild grey seal pups displayed the expected depressed glucose levels and elevated NEFA and ketone body levels during a 52-day fast (Nordøy, Ingebretsen & Blix, 1990; Nordøy & Blix, 1991). These results were similar to those found for two abandoned, and clearly emaciated, Steller sea lion pups in Alaska – both showed elevated ketone and fatty acid levels indicative of Phase II starvation when fat stores are metabolized (Rea, 1995). Two other abandoned pups showed signs of Phase III starvation, demonstrating that these blood parameters are good indicators of nutritional stress in pinnipeds (Rea, 1995). Finally, Hubbard (1968) reported BUN levels in an anorexic juvenile Steller sea lion of 160 mg%, compared to normal values of 9–30 mg%.

Leukocyte counts are another potential measure of change in nutritional status. Thompson *et al.* (1997) discovered that leucocyte counts were lower during years of high gadid abundance (e.g. cod) in the diets of harbour seals in Europe *P. v. vitulina*, compared to years of high clupeid abundance (e.g. herring). These differences could be attributed to immunosuppression from differences in nutritional value or contamination levels of prey, or to differing pathogen contents in the water between years and regions. Thompson *et al.* (1997) also found evidence of widespread macrocytic anaemia in harbour seals during years of high gadid consumption, which could be because of acclimation to that diet or differences in the nutritional quality of the prey.

Behavioural and physiological modifications

When faced with food shortages or poor quality food, animals will modify certain behaviours to reduce nutritional stress and conserve energy and body condition. For example, rats fed low-fat diets *ad libitum* will maintain body mass by increasing daily food intake, thereby compensating for a poor quality diet (Harris, 1991; Donnelly, Kitts & Trites, 2003). If mammals cannot compensate by increasing their food intake, they may depress their metabolism, reduce activity levels or increase foraging effort (Rosen & Trites, 1999).

Metabolic depression (decreased basal metabolic rate) has been documented in northern fur seals, grey seals, harbour seals and Steller sea lions during periods of fasting or restricted food intake (e.g. Miller, 1978; Nordøy *et al.*, 1990; Markussen, 1995; Rosen & Trites, 1999). Captive northern fur seal pups were found to reduce their basal metabolism by half within a week of the onset of fasting (Miller, 1978). This reduction was attributed to depressed cellular metabolism rather than to a loss of metabolic tissue through weight loss. When transferred from an energy-dense diet (meaning a high-fat/high-calorie diet) to a low-fat diet, the resting metabolic rate of captive Steller sea lions decreased by 10% after 1 week, and by 24% after 2 weeks (Rosen & Trites, 1999). Metabolic depression is a strategy used to reduce energetic requirements and compensate for nutritional deficiencies (Øritsland & Markussen, 1990).

Many studies have documented changes in the length of foraging trips relative to prey density and distribution. Lactating Antarctic fur seals, for example, have been shown to adjust the lengths of their trips in response to changes in krill abundance, making longer trips and expending more energy when prey are scarce, and making shorter trips and spending more time ashore when prey are abundant (Boyd *et al.*, 1994b; McCafferty *et al.*, 1998; Boyd, 1999). During the 1983 El Niño when prey were scarce, South American fur seals in Peru exhibited longer feeding trips (4 vs. 3 days) and made more frequent deep dives (Majluf, 1991). Galapagos fur seals also increased the time they spent foraging when prey were scarce, subsequently lengthening their time away from their sedentary pups on the beach. These longer foraging periods were presumably energetically costly for the females, and resulted in starvation of their unattended pups (Trillmich & Dellinger, 1991). In California, the length of foraging trips by lactating northern fur seals increased significantly during El Niño years. California sea lions also increased the length of their foraging periods (1.7–3.9 days) as well as the amount of time they spent at sea (5% increase in 1983 over 1982) (Heath *et al.*, 1991). During such food shortages, consistent behavioural modifications were clearly documented among many species of pinnipeds.

Summary – Pinnipeds

Inadequate nutrition can affect pinnipeds in a number of ways. As with all mammals, reduced energy intake leads to a loss of body weight and may stunt body growth. However, ovulation and fertilization appear to be more resistant to nutritional stress in pinnipeds than in other mammals. This may be a function of their reproduction strategy of delayed implantation. Pinniped foetuses are more likely to be aborted in the late stages of pregnancy, leading to reduced numbers of pups being born when food is scarce. Mortality of nursing pups increases if lactating females are unable to acquire sufficient prey to produce milk. Young and recently weaned pinnipeds are more susceptible to the effects of starvation than older and more experienced foragers because of their higher relative energy needs and inexperience. Juvenile mortality is therefore expected to be high during times of nutritional stress.

A decline in numbers of pups born or survival of juveniles is not proof of nutritional stress, given that predation by sharks and killer whales can increase the mortality of young, and disease can negatively affect both reproduction and survival. More convincing confirmations of a nutritional problem include reductions in body sizes and changes in blood chemistry and tissue composition. Behavioural and physiological modifications are other indicators of changes in feeding conditions. Pinnipeds appear to reduce their metabolism (metabolic depression) and become less active on shore when food intake is restricted, and have been shown to increase the length of time they spend searching for prey at sea.

It is noteworthy that most of the effects of nutritional stress on pinnipeds summarized above were observed under *extreme* circumstances and drastic food shortages, such as the 1983 El Niño. A milder 1976 El Niño did not result in such mass starvation or reduced natality of Galapagos sea lions (Trillmich & Limberger, 1985). Just how large the nutritional insult must be to noticeably affect blood chemistry, behaviour, growth, survival and reproduction is not known; nor is it known if these changes occur in progressive and predictable manners.

EVIDENCE FOR NUTRITIONAL STRESS IN STELLER SEA LIONS

The question at hand is whether Steller sea lions in Alaska exhibited definitive signs and symptoms of nutritional stress during their rapid (1980s) and moderate (1990s) population decline (Fig. 1). If so, a secondary question is whether this ‘stress’ was because of reduced quantity or quality of their prey. The following reviews the evidence for nutritional stress.

Reduced body size – non-pups

Data on body size of non-pups were only collected during two periods in the Gulf of Alaska (at the start of the decline from 1975 to 1978, and during the decline from 1985 to 1986) (Calkins & Pitcher, 1982; Calkins & Goodwin, 1988; Winship, Trites & Calkins, 2001). They suggest that body weights, standard lengths and axillary girths were all significantly smaller in animals aged 1–10 years during the population decline (1985–86) than at the start of the decline (1975–78) (Calkins & Goodwin, 1988). These changes were independent of reproductive status in females. In 1985–86, sea lions 1–5 years old were 4.5% shorter and 22.5% lighter than those in the 1970s, and animals 6–10 years of age were 1.2% shorter and 6.9% lighter (Lowry, Frost & Loughlin, 1988).

Theories of density-dependent responses predict that body size should have increased as population density decreased and *per capita* food increased. The fact that body size decreased during this decline suggests that *per capita* food decreased in either availability or quality (Calkins & Goodwin, 1988). Such a response further suggests that the carrying capacity for Steller sea lions may be lower now than it was in the past.

A re-examination of the original Calkins & Goodwin data set by Castellini & Calkins (1993) corroborated the conclusion that sea lions were shorter, lighter and thinner in the 1980s than in the 1970s. However, they also noted that the sea lions had less body fat and/or a different body shape as determined by body volume/weight relationships. Such observations are expected for animals that are nutritionally stressed. Furthermore, this reduction in body size seemed to be more apparent in juvenile sea lions than in adults, implying slower growth of the younger individuals because of limited food resources (Sease & Merrick, 1997). Further use of multiple regression models on the length, girth and weight measurements supported the notion that the greatest reductions in size were among the youngest animals (Calkins, Becker & Pitcher, 1998) (Table 1).

Body length is believed to reflect nutritional status during the first 8–9 years of life, while weight and girth likely reflect more immediate nutritional condition, in addition to lifetime nutrition (Calkins & Pitcher, 1982). It appears that younger animals (Table 1) were more nutritionally stressed than adult sea lions at the time of measurement in the 1980s, as seen by the larger reductions in their weights and girths compared to the older animals.

Contradictory data from the 1990s compared the size and body condition of 25 adult females in declining populations (Chirikof Island and Fish Island; Fig. 2) with adults in a stable population (Forrester Island) (Davis *et al.*, 1996b). No significant differences were found among the geographical areas in standard length, axillary girth or weight of mature females. Furthermore, body compositions did not differ, with total body fat averaging 8.3% of total body weight. One explanation for these results is that the samples may have been biased and only reflected healthy mothers that maintained pregnancies over the winter. Another is that adult sea lions were equally able to meet their energetic needs in both regions. Thus, it is conceivable that nutritional stress decreased for mature females as the rate of population decline slowed (Sease & Loughlin, 1999). However, it is not possible to infer whether the same was true for juveniles.

In summary, it has been demonstrated that juvenile and adult Steller sea lions were physically smaller during the population decline (1980s) than they were before the decline (1970s). This holds true for morphometric measurements (length, girth and weight) and for body condition indices, and is consistent with the hypothesis that the Steller sea lion population decline was caused by nutritional stress. Data from the 1990s are not directly compa-

Table 1. Reductions in axillary girth and weight in Steller sea lions aged 1, 7 and 14 years in 1985–86 as compared to 1975–78 (Calkins *et al.*, 1998)

Age (years)	Reduction in axillary girth (%)	Reduction in weight (%)
1	10.4	26.9
7	6.29	12.3
14	1.7	3.0

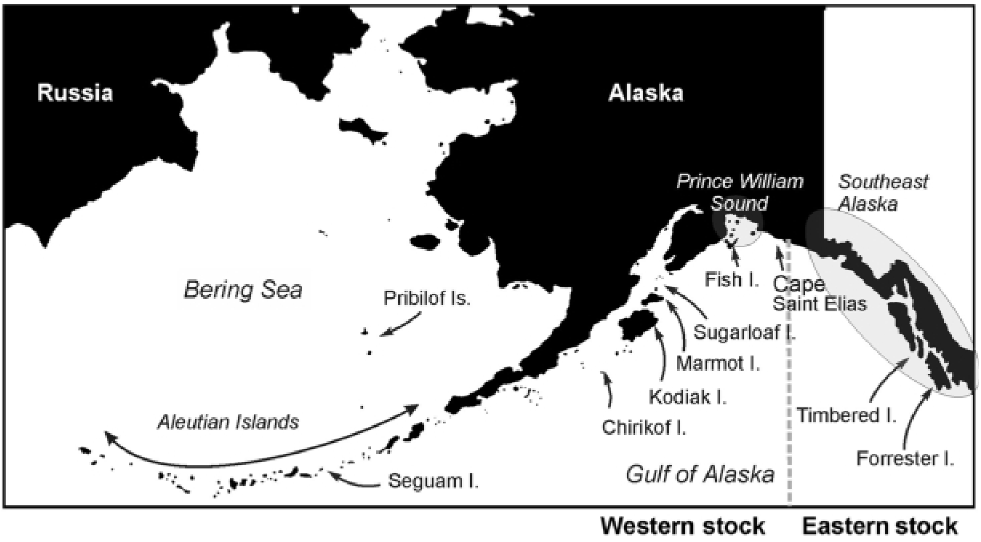


Fig. 2. Locations of major Steller sea lion rookeries and haulouts cited in the text. The dashed line shows the division between the declining (western) and increasing (eastern) populations of Steller sea lions in Alaska.

rable with the earlier data sets, but suggest that adult females may have obtained adequate nutrition in more recent times.

Reduced productivity

Fertility parameters such as delayed first oestrus, anoestrus (temporary cessation of the oestrous cycle) and pregnancy rates before parturition are difficult to measure in wild populations of sea lions. Despite this, some data regarding abortion rates and pregnancy rates before and during the Steller sea lion decline are available. The most common measures of fertility in these populations, however, are pup counts.

Counting pups (<1 month old) is the simplest way to measure reproductive success from one year to the next. They remain on or near shore during the early nursing period, and are easy to count. Approximately 45% fewer pups were counted in the 1980s than in the 1970s (Calkins & Pitcher, 1982; Calkins & Goodwin, 1988). However, it is unclear whether reduced birth rates or fewer female recruits might have contributed to this decline.

Examining the reproductive organs (ovaries, uteri, etc.) of Steller sea lions yielded estimates of early term pregnancy rates of 95% and 92% in the 1970s and 1980s, respectively, and mid- to late-term pregnancy rates of 67% and 60%, respectively (Calkins & Goodwin, 1988). Neither of these comparisons was statistically different between years. However, the substantial failure of pregnancies over the winter in both periods implies that summer conditions may not be stressful, but that nutrition is more critical later in gestation when the energetic costs of pregnancy are much higher (Winship *et al.*, 2002). The surprisingly high failure of pregnancies (33–40%) have led some to suggest that nutrition was likely inadequate by the mid-1970s (Calkins *et al.*, 1998).

Pitcher *et al.* (1998) further analysed reproductive data from the 1970s and 1980s to compare the pregnancy rates of lactating and non-lactating females. They noted that although absolute pregnancy rates did not differ significantly between the 1970s and 1980s, the rates did differ when lactation status was considered (i.e. pregnancy rates declined among lactating females during the 1980s).

Most Steller sea lion pups do not appear to wean until they are almost a full year old (Trites *et al.*, 2001). This means that females that rear pups every year will nurse one pup while pregnant with their next. In the 1970s, lactation status did not appear to affect the probability of a female being pregnant, implying that she was able to obtain sufficient food to nurse one pup and maintain a second pregnancy simultaneously. In the 1980s, however, a female's probability of being pregnant was greatly reduced if she was nursing a pup from the previous year. The reduced body condition of females in the 1980s (Calkins & Goodwin, 1988), combined with the positive correlation between pregnancy status and indices of weight and blubber thickness (Pitcher *et al.*, 1998), could have reduced the numbers of pups born and contributed to the population decline of Steller sea lions.

Records of abortions and failed pregnancies are another commonly used index of reproductive success. Reproductive failure is defined as resorption of an embryo, abortion or a missed pregnancy where the female did ovulate but either fertilization or implantation failed (Calkins & Goodwin, 1988). Aborted foetuses have been reported during winter observations of haulout sites (e.g. Porter, 1997), but the available data are too scant to draw any meaningful conclusions.

Birth weights and growth rates

Data are insufficient to conclude whether birth weights of Steller sea lions were reduced during the population decline. Nor are there data to compare pup growth rates during the 1970s and 1980s. However, during the 1990s, the weights of a small sample of newborn pups at Forrester Island were compared with a similar sample from the declining populations of Chirikof, Marmot, Fish and the Aleutian Islands (Davis *et al.*, 1996a; Adams, 2000). No significant difference was found among locations in the first 2 days of life (pups averaged 21.8 kg; Adams, 2000). There was also no difference in the proximate composition of mothers' milk, or in the lean body weight and total body fat between pups at the different locations. However, pups from the declining areas grew faster (0.41 kg/day) than those in the stable population (0.25 kg/day), and required half as much milk energy (Adams, 2000). These findings suggest that newborn pups and their mothers were not nutritionally stressed during summer during the 1990s at the declining sites (Brandon *et al.*, 1996; Davis *et al.*, 1996b; Adams, 2000; Brandon, 2000).

Large numbers of older pups (2–6 weeks old) weighed during the 1980s and 1990s were found to be heavier at declining rookeries (Aleutian Islands and Gulf of Alaska) compared to increasing and stable sites (Southeast Alaska) (Merrick *et al.*, 1995; Rea, 1995). Rea (1995) found that Aleutian Island pups had higher body condition indices [girth/length] and lower density indices [mass/(length × girth^2)], meaning that they were fatter and heavier for their length than pups in the Gulf of Alaska. This again suggests that adult females obtained adequate nutrition during the 1990s and were able to produce sufficient milk for their pups.

The differences in pup weights and growth rates between the different regions in the 1990s do not support the hypothesis that pups and their mothers from the declining population were nutritionally stressed during the summer. It should be kept in mind, however, that a healthy condition at 5 or 30 days of age does not ensure successful weaning, survival or foraging efficiency later in life (Rea, 1995).

Reduced pup survival

Despite occasional sightings of abandoned pups on Alaskan rookeries and haulouts (Rea, 1995; Porter, 1997; Rea *et al.*, 1998; Milette, 1999), there is no evidence of high mortality of pups either before or after the population decline. Yet, large numbers of dead pups should have been observed on rookeries if severe shortages of prey were occurring. Females should have ceased nursing if they were unable to find sufficient prey, even if resources had been adequate in the previous spring and winter to allow for the birth of relatively healthy pups.

Reduced juvenile survival

Concern about juvenile survival dates back to the first large-scale Steller sea lion surveys by Calkins & Goodwin (1988). The observed rate of decline in adults coupled with an apparent increase in the average age of adult females was one of the first indications that the younger age classes might be at risk. In the Marmot Island population, for example, the average age of females over 3 years of age increased by 1.55 years between 1975–78 and 1985–86 (Alaska Sea Grant, 1993). Subsequent modelling studies indicated that the observed population decline could be because of a 10–20% decrease in juvenile (0–3 years) survival, in addition to a 1–2% decrease in adult survival (York, 1994). Other models suggested that the observed decline could have only occurred if 3000–3500 females aged 1–7 years were removed from the population every year for the past 30 years (Alaska Sea Grant, 1993). The observations of decreasing numbers of young animals coupled with the modelling exercises have led some to conclude that the population decline could have been caused by reduced survival of juveniles, with no reduction in female fertility (Loughlin, 1998).

Direct evidence of low juvenile survival resulted from a mark–resighting experiment in 1987–88 and 1992 (Fritz, Ferrero & Berg, 1995). In 1992, 424 female pups were tagged before weaning. While approximately 100 of the marked females were expected to return to their rookery of birth in 3–4 years, only 15 were sighted. A similar study in which 800 sea lion pups were branded in 1987–88 on Marmot Island also yielded subadult and adult (5–10 year old) returns that were an order of magnitude lower than expected (Sease & Merrick, 1997). More recent analyses of resighting data also reported significantly fewer branded animals at Marmot Island compared to Forrester Island where the population had increased, which suggests that survival rates were lower in the western stock (Raum-Suryan *et al*., 2002).

Reduced proportions of juveniles relative to adults at haulouts and rookeries provide additional evidence that inadequate juvenile survival may have contributed, and may still be contributing, to the decline. For example, at Marmot Island in the Gulf of Alaska, proportions of juveniles counted in June dropped from 15–20% in the 1970s to 5% or less in the 1990s (Sease & Merrick, 1997). Such changes might reflect a decrease in survival of juveniles, a change in pregnancy rates or some other factors, and highlight the need to be cautious when interpreting counts of juveniles or non-pups (Calkins, Pendleton & Pitcher, 1996).

Blood parameters

Evidence of nutritional stress in Steller sea lions based on blood chemistry is presently inconclusive. A comparison of haemoglobin values and packed cell volumes in the 1970s and 1980s found both to be lower in the decline period, although only haemoglobin levels were significantly different (Calkins & Goodwin, 1988). Lowered haemoglobin values were interpreted to indicate widespread clinical anaemia because of nutritional stress. It was considered unlikely to be because of blood loss via parasitic insult or chronic bleeding, and more likely a result of vitamin and mineral deficiencies, failure of intestinal absorption and/or hypoproteinaemia in a deficient diet.

Haptoglobin is one of a group of blood proteins that increases markedly in response to infection, inflammation, trauma or tumours, in what is known as the acute phase reaction (Zenteno-Savin *et al*., 1997). Analysis for this protein is non-specific with respect to the cause of the stressor, but is very sensitive and useful in diagnosing the health of many mammals.

Levels of haptoglobin in Steller sea lions were significantly higher in animals of all ages from the declining populations (Zenteno-Savin *et al*., 1997). They were also found to be higher for harbour seals from Prince William Sound (declining) than from Southeast Alaska (increasing) (Zenteno-Savin *et al*., 1997). This is some of the first evidence from blood chemistry that one or more stressors may have initiated an acute phase reaction in Steller sea lions.

For newborn sea lions, blood testing for metabolic parameters has not detected any sign that this age group is nutritionally stressed. Normal blood ketone body levels, glucose levels and BUN levels were found in neonates on Marmot Island in 1990 and 1991 (Castellini *et al*., 1993), contrary to the hypothesis that they were food restricted. Similar measurements in the Aleutian Islands, Gulf of Alaska and Southeast Alaska have also failed to indicate any evidence of nutritional stress in pups from declining areas, and suggest superior condition of these young in 1990–96 (Rea *et al*., 1998).

Behavioural and physiological modifications

As we previously noted, pinnipeds faced with limited food sources will typically increase their foraging effort, increase foraging trip lengths, decrease the perinatal period (time from parturition to mother's first feeding trip), depress metabolic rates and provide less care (nursing) for pups. Studies measuring similar parameters in Steller sea lions in Alaska are relatively few, and most were conducted from the mid- to late 1990s after the rate of population decline slowed significantly.

Comparisons of maternal attendance patterns and foraging behaviour were made between animals at Sugarloaf Island (declining population) and Forrester Island (a large and stable population) in 1994 and 1995 (Milette & Trites, in press). Counter to expectations, lactating females at the declining Sugarloaf population, which were assumed to be food-limited, had longer perinatal times and spent more time on shore with their pups than those in the increasing population. Foraging trips were also significantly shorter at Sugarloaf Island compared to Forrester Island (19.0 h vs. 25.6 h), and lactating females spent less time foraging at sea (35.9% vs. 38.9%, respectively). Such differences were independently supported by telemetry studies conducted by Brandon (2000). All of these behaviours suggest that females in the declining population did not have difficulty finding prey during summer.

Andrews *et al.* (1999, 2002) tracked a few lactating females at Seguam Island (declining population) and compared them with a similar group of females from the large and stable Forrester Island population. They also found that females from the declining population made significantly shorter feeding trips compared to those from the increasing population (7 h vs. 48 h). The average length of time for females to capture their first fish was less than 1 h at Seguam Island and about 5 h at Forrester Island. These findings suggest that prey were more obtainable for the declining population than for the Forrester Island population.

Behavioural observations during winter indicate that lactating females spend twice as much time away from their haulouts as they do during summer (Trites & Porter, 2002). Attendance cycles averaged 24 h on shore and 48 h at sea during the winter. However, there was no apparent difference between average winter attendance cycles of animals from the declining (Marmot Island and Cape St. Elias) and increasing haulout populations (Timbered Island) (Trites *et al*., 2001).

Summary – Steller sea lions

There are two primary sets of field data that shed light on the nutritional stress hypothesis. The first was collected from two samples of Steller sea lions shot in the Gulf of Alaska (during the 1970s at the start of the decline, and during the 1980s at the peak of the decline). The second set was collected using a number of different techniques during the 1990s in the regions of population increase (Southeast Alaska) and population decline (Aleutian Islands and Gulf of Alaska).

Comparing the samples of sea lions shot in the 1970s and 1980s suggests that animals were physically smaller in the 1980s, and that the effect was more pronounced in younger animals than in older ones. A shift in age structure and a lower than expected return of marked sea lions further suggest a concurrent increase in juvenile mortality. Pregnancy rates also appear to have declined over this period, and increased haptoglobin levels were detected, both of which are indicative of nutritional stress.

The consequences for juveniles faced with limited food are starvation (not detected), increased susceptibility to disease or predation (unknown), or reduced growth rate (detected). Increased mortality directly affects population numbers, but reduced individual growth rates have indirect and less obvious effects. Slower body growth may delay maturation and the onset of oestrous cycling. Such a delay could result in females not having pups for an additional year or two, which would delay their contribution to population growth. This alone may not have caused the decline, but could certainly have contributed to it and also have hindered its recovery.

Most of the data collected in the 1990s were not directly comparable with those collected in the 1970s and 1980s. The 1990s studies tended to focus on lactating females and their dependent offspring during summer. A data set comparable to the 1970s and 1980s would have required shooting another random sample of sea lions, and would not have been justifiable given the endangered status of this population. The 1990s studies suggest that summer conditions for lactating females were superior in the declining population compared to the increasing population. Pups grew faster and were physically larger in the Gulf of Alaska and Aleutian Islands than in Southeast Alaska, while blood chemistries of pups were normal in both regions. Lactating females also made shorter feeding trips than predicted in the area of decline and spent more time on shore with their pups during summer. Foraging trips of lactating females were longer in winter, but did not appear to differ significantly between regions. The only suggestion of a possible nutritional problem in the 1990s was higher haptoglobin levels among non-pups in the declining regions compared to the increasing populations of Southeast Alaska.

In summary, the data available for the 1970s and 1980s are consistent with the hypothesis that Steller sea lions, particularly the juvenile age classes, were nutritionally compromised. Data collected during the 1990s suggest that lactating females and their dependent offspring acquired adequate nutrition during the summer. Those data do not provide new information about the relative health of juveniles or the conditions and pregnancy rates of mature females during winter and spring. Only blood chemistries (i.e. higher haptoglobin levels) suggest higher stress levels during the 1990s in the declining population, but the source of this stress is unknown.

QUANTITY VS. QUALITY OF PREY

Nutritional quality vs. quantity of prey is a subtle, but complex, component of the nutritional stress hypothesis. One view holds that the quantity of prey available to the declining population of Steller sea lions was high overall, but because of the species composition of available prey (primarily gadids), the diet was nutritionally inferior – the junk food hypothesis (Alverson, 1992; Rosen & Trites, 2000b). An alternative view is that gadids are nutritionally adequate, but are not available in sufficient numbers because of fishing or some other factor (Merrick, 1995; NMFS, 2001). Either possibility would detrimentally affect juvenile sea lions more than mature individuals, because of their higher relative energy requirements (Winship *et al.*, 2002) and relative inexperience at foraging (Merrick & Loughlin, 1997).

Quantity of gadids and forage fish

The available information suggests that forage fish such as Pacific herring *Clupea pallasi* and capelin *Mallotus villosus* were relatively abundant before the decline of Steller sea lions compared to walleye pollock *Theragra chalcogramma* and Pacific cod *Gadus macrocephalus* (Alverson, 1992; Anderson, Blackburn & Johnson, 1997; Trites *et al.*, 1999; NMFS, 2001). Diet information suggests that before the decline, sea lions ate primarily small forage fish such as herring. Scat and stomach content analyses in the Kodiak Island area in the 1970s revealed a summer diet consisting primarily of herring, with smaller amounts of gadids and salmon *Oncorhynchus* spp. During the decline, however, their primary diet consisted of gadids such as pollock and cod (60%), supplemented with forage fish, cephalopods, salmon and flatfish (Pleuronectidae) (Table 2). This noticeable switch in diet composition during the population decline was concurrent with an increase in the dominance of flatfish and gadids in the ecosystem through the 1970s–1990s (Anderson *et al.*, 1997; Trites *et al.*, 1999; Benson & Trites, 2002).

Sea lions from colonies in the area of decline primarily fed on walleye pollock and Atka mackerel *Pleurogrammus monopterygius* (a hexagrammid related to lingcod) during the 1980s and 1990s (Merrick *et al.*, 1987; Merrick, Chumbley & Byrd, 1997). Those in stable regions preyed on a more diverse diet of Pacific herring, Pacific sand lance *Ammodytes hexapterus* and various smelts (Osmeridae spp.). The high abundance of gadids in declining regions may be partially responsible for the reductions in Steller sea lion body size, and for the shorter foraging trips observed. Pinnipeds are probably opportunistic feeders (Geraci, 1975), and are unlikely to forego large quantities of pollock to search for less available fish, even if gadids are inferior in quality (cf. Thomas & Thorne, 2001).

Quality of forage fish

Small schooling fish, such as Pacific herring, which appear to have dominated the diet before the Steller sea lion decline, are seasonal feeders that build up large fat reserves to overwinter without feeding. Thus their body composition fluctuates substantially throughout the year (Perez, 1994). Generally, herring are referred to as 'fatty' fish (oil 5–15%, protein 15–20%) (Stansby, 1969), with an average body fat content of approximately 12.8% (range 2.2–24%) (Walford & Wilber, 1955; Stansby, 1976; Alverson, 1992). The energetic density of herring has been estimated to range from 7.28 to 9.86 kJ/g of wet mass, but varies among seasons, age classes, reproductive status and locations (Perez, 1994; Rosen & Trites, 1999).

Table 2. Proportion of Steller sea lion scats and stomachs containing five prey categories during the summer months in the declining Kodiak Island region in the 1970s, 1980s and 1990s (Merrick *et al.*, 1997)

	Gadids (%)	Salmon (%)	Small schooling fish (%)	Cephalopods (%)	Flatfish (%)
1990–93	85.2	18.5	18.5	11.1	13.0
1985–86	60.0	20.0	20.0	20.0	5.0
1976–78	32.1	17.9	60.7	0.0	0.0

Gadids – walleye pollock, Pacific cod, Pacific hake; Small schooling fish – capelin, Pacific herring, eulachon and Pacific sand lance; Flatfish – arrowtooth flounder, rock sole.

Herring has been used in laboratory studies to test the comparative nutritional quality of different fish species, and has always emerged as an excellent source of protein and fat that promotes rapid growth without noticeable ill side-effects (Privett *et al.*, 1960; Lawson *et al.*, 1997a; Rosen & Trites, 1997, 2000a,b; Donnelly *et al.*, 2003). Digestibility of herring is also higher than that of many other species of fish. For example, digestibility of herring fed to captive ringed seals *Phoca hispida* was 94%, and was higher than values for Arctic cod *Boreogadus saida* (88%), capelin (87%) and rockfish (*Sebastes* spp.) (83%) (Lawson *et al.*, 1997a). Herring is one of the most commonly used foods in marine aquariums, and with supplementation of the appropriate vitamins and minerals, has proven to be a successful diet for captive pinnipeds (Geraci, 1975).

Quality of gadids

Gadids became the primary prey species for Steller sea lions in the area of population decline since the early 1980s. They are a large family of fishes that includes many species such as walleye pollock, Pacific cod, saffron cod *Eleginus gracilis*, Pacific tomcod *Microgadus proximus*, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus* and hake *Urophycis* spp., most of which are eaten by sea lions (Calkins & Pitcher, 1982). Gadids are generally referred to as 'nonfatty' or 'lean' fish (oil < 5%, protein 15–20%) with reported energy densities ranging from 4.54 to 4.72 kJ/g wet mass (Table 3) (Walford & Wilber, 1955; Stansby, 1969; Perez, 1994; Rosen & Trites, 2000a). Composition analyses (Table 3) show that the primary difference between gadids and herring is fat content, which determines the amount of energy available to sea lions. Energy densities of gadids are only 70–80% of those of herring.

Pollock and other gadids are undoubtedly lean fish, but additional qualities also render them less nutritious for pinnipeds. When juvenile harp seals were switched from a diet of Atlantic herring to Atlantic pollock, the seals' body fat content declined by 32% over 30 days while their body protein increased in proportion to protein intake (Kirsch, Iverson & Bowen, 2000). This loss of body fat occurred despite normal food intakes of approximately 6.5 kg/day, and reflected a change in body composition (reduced fat and increased protein) vs. body mass. This implies that marine mammals (particularly young and growing individuals) may not be able to maintain adequate energy reserves on pollock diets despite large intakes. Reductions in body fat caused by eating large amounts of pollock could be detrimental to animals residing in cold environments and subject to periodic fasts between foraging bouts. Concurrent increases in body protein content could be energetically expensive as protein is metabolically active and increases an animal's caloric requirements.

A short-term feeding experiment found that six young Steller sea lions lost approximately 0.6 kg/day when their diet was switched from herring to pollock for 11–23 days (Rosen & Trites, 2000b). The young animals did not increase their energy intake sufficiently to compensate for the low caloric content of pollock despite being allowed to eat as much pollock

	Oil (%)	Protein (%)	Energy density (kJ/g wet mass)
Pollock	0.8	20	4.66
Cod	0.4	17	3.95
Whiting	0.4	17	–
Haddock	0.3	18	–
Herring	11.0	19	8.61

Table 3. Partial composition analyses and energy densities of herring and common gadids (Walford & Wilber, 1955; Perez, 1994)

as they wanted. A similar result was found when they were fed low-fat squid (intake was approximately 7 kg/day) (Rosen & Trites, 1999). Loss in body weight was accompanied by suppression of mass-specific resting metabolic rate, indicating a fasting or nutritionally stressed state. Failure to increase food intake was unexpected and might have been related to factors that determine satiation.

The energy required to digest a meal of pollock (the heat increment of feeding, HIF) is higher than that required to digest a similar size meal of herring (15.7% vs. 11.9% of gross energy intake, respectively) (Rosen & Trites, 1997). Additionally, larger meals are more energetically expensive to consume than smaller meals (Rosen & Trites, 2000b), which would be costly to an animal attempting to eat more food to compensate for low fat content. The loss of body mass in Steller sea lions eating pollock is thus attributable to many factors including the lower energy content of pollock, a higher HIF of pollock than herring and the need to compensate for low energy values of pollock. This means that a Steller sea lion would have to consume 35–80% more pollock than herring to obtain an equal number of calories (Rosen & Trites, 2000b).

Negative responses to switching diets from high-energy forage fish (clupeids such as herring and sprat *Sprattus sprattus*) to gadids have also been documented in wild harbour seals in Scotland. Blood leucocyte counts were significantly elevated during years when Herring and sprat occurrence in the diet was low (1989–92) compared to years when they were the major dietary species (1987–89 & 1993–95) (Thompson *et al.*, 1997). This could be due to immunosuppression because of differences in prey contaminant or nutrient levels, or it could be due to differences in water quality between years and between foraging sites. More notably, when the seals switched to a primarily gadid diet, there was evidence of widespread macrocytic anaemia, thought to be related to differences in the nutritional quality of the prey. Iron levels in white flesh fish such as gadids are lower than in darker flesh fish (Geraci, 1975), and might explain the anaemic conditions.

Complications in iron absorption have been reported in mink that were fed gadids, such as hake and whiting. This results in a condition known as ‘cotton-fur’, and is a syndrome characterized by animals that are often emaciated and smaller than their non-cotton-fur counterparts, and whose underfur is uncharacteristically light in colour because of lack of pigmentation (Stout, Oldfield & Adair, 1960). In one study, the inclusion of hake and whiting in mink diets resulted in reduced size of animals and fur depigmentation proportional to the amount of gadids in the diet (Stout *et al.*, 1960). Similarly, mink that were fed diets including 30% hake suffered from lower lifetime weight gain and possible impaired iron absorption as indicated by lower levels of stored iron in the spleen and liver (Rouvinen, Anderson & Alward, 1997).

It is not clear to what extent the results of captive studies that found iron deficiency and poor fur quality can be extrapolated to wild animals, given that only one of the above studies was conducted in the wild. Furthermore, impaired iron absorption in the mink may be a function of the hake having been frozen. When hake were either cooked or fed fresh, the cotton-fur disorder was less apparent, if present at all (Costley, 1970). The factor causing cotton-fur is hypothesized to be formaldehyde, a secondary by-product of lipid oxidation that is not present in fresh fish, nor applicable to feeding in the wild.

Walleye pollock protein fed to rats resulted in alteration and partial destruction of kidney and liver tissues, the extent of which was related to the amount of protein in the diet (Gulich, Onoprienko & Sokolova, 1990). However, it is not known whether the toxicity was because of the protein itself, or was because of by-products (acetyline amino acids) of the processing methodology.

Factors other than body composition and vitamin and mineral content can affect the nutritional value of a diet. The digestive efficiency of diets may reflect 'biologically available' nutrition. Juvenile Steller sea lions fed different diets of pollock, herring, squid and salmon revealed differences in digestive efficiency (percentage of prey energy retained) (Rosen & Trites, 2000a). The digestive efficiency appeared to have some relationship with energy density, being greatest for herring (95.4%), followed by pollock (93.9%), salmon (93.4%) and squid (90.4%).

Captive harp seals fed diets of Atlantic cod *Gadus morhua*, Arctic cod, Greenland halibut *Reinhardtius hippoglossoides*, Atlantic herring and capelin showed the lowest digestive efficiencies while consuming the low-fat gadids (93.5% for Atlantic and Arctic cod, vs. 94.7%, 95.7% and 96.6% for halibut, capelin and herring, respectively) (Lawson, Miller & Noseworthy, 1997b). Similar relationships between digestive efficiencies and energy content of the diet were found for kittiwakes *Rissa tridactyla* and thick-billed murres *Uria lomvia* fed capelin or cod (Brekke & Gabrielsen, 1994). This could potentially have contributed to the decline of marine birds that switched their prey from small forage fish to gadids (Anderson *et al.*, 1997).

All of the above results support the theory that pollock is less nutritious than herring, and that switching from a high quality, diverse diet including herring to one predominantly of pollock could place young Steller sea lions and other pinnipeds under nutritional stress.

CONCLUSIONS

Steller sea lions in central and western Alaska have undergone a dramatic population decline in the last 30 years (Fig. 1). The nutritional stress hypothesis holds that this decline was because of reduced availability of suitable prey (Alverson, 1992; Alaska Sea Grant, 1993; Rosen & Trites, 2000b; DeMaster & Atkinson, 2002), which may have been caused by reduced abundance of several important species of high-quality fish preyed upon by sea lions, such as herring and other small forage fish. The fish stocks that appear to have replaced the forage fish in the ecosystem and in the diets of Steller sea lions were predominantly gadids and flatfish (Merrick *et al.*, 1997; Trites *et al.*, 1999). If the nutritional value of all fish were equal, the newly abundant stocks of gadids and flatfish should have been able to support the sea lions. The continued decline of Steller sea lions in central and western Alaska suggests that these gadids may not have been as nutritious as the prey that were present in higher numbers before the decline, and that Steller sea lions and other pinnipeds are unable to flourish on low-fat/low-calorie prey.

The available data from Steller sea lions are consistent with the nutritional stress hypothesis, particularly during the 1980s when sea lions in Alaska were found to be smaller in length, girth and weight compared to animals before the decline (Calkins & Goodwin, 1988). This is most evident among the juvenile animals (ages 1–3 years), which are believed to be more susceptible to nutritional stress than adults or nursing pups. Other evidence of nutritional stress during the 1980s was an apparent increase in juvenile mortality (York, 1994), and a decrease in productivity as measured by pup counts and the incidence of failed pregnancies (Calkins & Goodwin, 1988). Lactating females also appeared to have been less likely to be pregnant than non-lactating females during the decline, indicating that the energetic stress of nursing while being pregnant with another pup may have prevented some females from giving birth each year (Pitcher, Calkins & Pendleton, 1998).

Support for the nutritional stress hypothesis during the 1990s is less conclusive than for the 1980s. This is largely because most of the studies conducted during the 1990s were not comparable with earlier studies, and were designed to compare increasing and decreasing regions of abundance rather than to compare pre- and post-decline conditions. This change in data collection procedures was partly because of the unacceptability of shooting endangered sea lions for comparison with samples of animals shot in the 1970s and 1980s. It might also be explained by an inadequate understanding that many researchers working in the 1990s had about the historical data. The 1990s studies revealed little, if anything, about nutritional conditions, other than during summer when they appeared good. Only haptoglobin and haemoglobin test results suggested possible continued nutritional stress during the 1990s (Calkins & Goodwin, 1988; Castellini *et al.*, 1993; Zenteno-Savin *et al.*, 1997; Rea *et al.*, 1998).

The strongest evidence that Steller sea lions continued to be nutritionally stressed comes from dietary studies that showed little change in their diets between the 1980s and 1990s. Pollock and Atka mackerel continued to dominate the diet of sea lions in the Gulf of Alaska and Aleutian Islands in the 1990s (Sinclair & Zeppelin, 2002). In contrast, Steller sea lion populations in Southeast Alaska increased throughout the 1990s, while consuming a higher diversity of prey (A.W. Trites and D.G. Calkins, unpublished data). Merrick *et al.* (1997) found a significant correlation between diet diversity and rates of population change in the early 1990s. Further examination of this relationship suggests that diet diversity was a proxy for energy content. Populations that had the highest rates of decline in the 1990s had the lowest dietary diversity and highest consumption requirements because of the low energy density of the prey they were consuming (Winship & Trites, 2003).

It should be kept in mind that a number of conclusions about changes in diet and body growth between the 1970s and 1980s were derived from *post-hoc* testing of data that were never collected with the intention of making such comparisons. As such, there are uncertainties concerning the compatibility and randomness of the samples drawn during these two eras. It is equally true that the majority of studies conducted during the 1970s, 1980s and 1990s are limited by their small sample sizes, restricted geographical ranges and associated caveats (which are discussed by the authors of the respective studies). Despite such shortcomings, however, these remain the only data available to help understand what happened to Steller sea lions.

It should be equally noted that most of the changes documented in the body sizes, births, deaths, physiologies and behaviours of other pinniped populations experiencing nutritional stress occurred during severe and brief shortages of prey (generally 1–3 years duration). In Alaska, the changes exhibited by Steller sea lions appear to be far more subtle than have been documented elsewhere, and may be indicative of a population that has experienced chronic nutritional stress (i.e. 20–30 years duration) rather than an acute nutritional insult (i.e. 1–3 years). Chronic nutritional stress may reflect reduced quality of prey rather than a decrease in quantity of prey.

Gadid biomass has been high in the Gulf of Alaska and Bering Sea during the sea lion decline, but gadids are less nutritious than small forage fishes (Geraci, 1975). The overall lower energy content of prey during this period, rather than the biomass of prey available, might effectively have set a lower carrying capacity for Steller sea lions. Captive and simulation studies question whether young Steller sea lions are physically capable of consuming 35–80% more gadids than those eating herring to achieve equal calories (Rosen & Trites, 2000b, 2002; Winship *et al.*, 2002). Possible toxic effects of gadids in the diets of pinnipeds are still under investigation, and may explain symptoms of anaemia in pinnipeds that fed on pollock (Calkins & Goodwin, 1988; Gulich *et al.*, 1990; Thompson *et al.*, 1997).

The changes observed in sea lions and their ecosystem are consistent with nutritional stress, but fall short of being a definitive test of the hypothesis. Whether or not the nutritional stress hypothesis is truly testable is debatable given how difficult it is to document changes that occur in the lower tail of the distribution of behaviours and responses of affected animals. The logistical difficulties of attaining large sample sizes in studies of Steller sea lions combined with the inherent problems of isolating a single effect from the multivariate array of factors that interact within an ecosystem make it unlikely that nutritional stress can be definitively demonstrated to be the underlying cause of the population decline. One is therefore left in the end to consider whether the preponderance of available evidence is consistent with the hypothesis.

In our opinion, results from the disparate sets of studies ranging from field to captive studies, to mathematical modelling, are supportive of one another, and suggest that the conditions experienced by Steller sea lions during the 1990s were consistent with continued nutritional stress. While it is important to be aware that conditions experienced by Steller sea lions may have changed in the 1990s (Pitcher, 2002), there is as yet no evidence to support this possibility. The apparent point of inflection in the decline of Steller sea lions in 1989 correlates with an oceanographic regime shift that influenced the composition of available prey, but these changes in the physical environment did not revert the ecosystem back to pre-decline conditions (Benson & Trites, 2002). The diet of Steller sea lions in the areas of population decline continues to be dominated by gadids or hexagramids (NMFS, 2001), and population changes consistent with chronic nutritional stress are likely to be more subtle and difficult to detect at low population sizes.

The data collected to date support the nutritional stress hypothesis as the major contributor to the Steller sea lion's decline in Alaska. With the exception of predation by killer whales *Orcinus orca* (Barrett-Lennard *et al.*, 1995; Matkin, Barrett-Lennard & Ellis, 2002), support for alternative hypotheses appears weak or non-existent (e.g. disease, shootings, competition with fisheries, incidental catch and others – NMFS, 1992, 2001), leaving nutritional stress as the most likely underlying explanation for the decline of Steller sea lions in Alaska. Efforts should be made to design studies and collect data that are comparable with earlier decades to allow for continued testing of the nutritional stress hypothesis, and for continued monitoring of the nutritional status of Steller sea lions.

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REFERENCES

Adams, T.C. (2000) Foraging differences and early maternal investment in adult female Alaskan Steller sea lions (*Eumetopias jubatus*). PhD Thesis, Texas A&M University, TX.

Alaska Sea Grant. (1993) Is it food? Addressing marine mammal and sea bird declines. *University of Alaska Fairbanks, Alaska Sea Grant Report 93–01.* University of Alaska Fairbanks, Fairbanks, AK.

Alverson, D.L. (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Reviews in Aquatic Sciences*, **6**, 203–256.

Anderson, P.J., Blackburn, J.E. & Johnson, B.A. (1997) Declines of forage species in the Gulf of Alaska, 1972–1995, as an indicator of regime shift. *Forage Fishes in Marine Ecosystems*, pp. 531–543. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks, AK.

Andrews, R.D., Calkins, D.G., Davis, R.W., Loughlin, T.R., Norcross, B.L., Peijnenberg, K. & Trites, A.W. (1999) A comparison of the foraging ecology of Steller sea lions from declining and stable populations, [abstract]. *13th Biennial Conference on the Biology of Marine Mammals*, pp. 6–7. Maui, HI.

Andrews, R.D., Calkins, D.G., Davis, R.W., Norcross, B.L., Peijnenberg, K. & Trites, A.W. (2002) Foraging behavior and energetics of adult female Steller sea lions. In: *Steller Sea Lion Decline: Is it Food II* (Ed. by D. DeMaster & S. Atkinson), pp. 19–22. University of Alaska Sea Grant, AK-SG-02–02, Fairbanks, AK.

Barash, I.A., Cheung, C.C., Weigle, D.S., Ren, H., Kabigting, E.B., Kuijper, J.L., Clifton, D.K. & Steiner, R.A. (1996) Leptin is a metabolic signal to the reproductive system. *Endocrinology*, **137**, 3144–3147.

Barb, C.R., Barrett, J.B., Rampacek, G.B. & Kraeling, R.R. (1998) Effects of metabolic fuel restriction on patterns of LH and GH secretion and serum leptin concentrations in the prepuberal gilt. *Journal of Dairy Science*, **81**, 230.

Barrett-Lennard, L.G., Heise, K., Saulitis, E., Ellis, G. & Matkin, C. (1995) *The Impact of Killer Whale Predation on Steller Sea Lion Populations in British Columbia and Alaska*, p. 77. University of British Columbia, Fisheries Centre, Vancouver, British Columbia, Canada.

Benson, A.J. & Trites, A.W. (2002) A review of the effects of regime shifts on the production domains in the eastern North Pacific Ocean. *Fish and Fisheries*, **3**, 95–113.

Bigg, M.A. (1988) Status of the Steller Sea Lion, *Eumetopias jubatus*, in Canada. *Canadian Field-Naturalist*, **102**, 315–336.

Booth, P.J. (1990) Metabolic influences on hypothalamic-pituitary-ovarian function in the pig. *Journal of Reproduction and Fertility*, supplement, **40**, 89–100.

Boyd, I.L. (1996) Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: the role of environment, age, and sex of fetus. *Journal of Mammalogy*, **77**, 124–133.

Boyd, I.L. (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behavioural Ecology*, **10**, 198–208.

Boyd, I.L. (2002) Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *Journal of Applied Ecology*, **39**, 103–119.

Boyd, I.L., Arnbom, T.A. & Fedak, M.A. (1994a) Biomass and energy consumption of the South Georgia population of southern elephant seals. In: *Elephant Seals: Population Ecology, Behavior, and Physiology* (Ed. by B.J. Le Boeuf & R.M. Laws), pp. 98–117. University of California Press, Berkeley, CA.

Boyd, I.L., Arnould, J.P.Y., Barton, T. & Croxall, J.P. (1994b) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology*, **63**, 703–713.

Braham, H.W., Everitt, R.D. & Rugh, D.J. (1980) Northern sea lion decline in the eastern Aleutian Islands. *Journal of Wildlife Management*, **44**, 25–33.

Brandon, E.A.A. (2000) Maternal investment in Steller sea lions in Alaska. PhD Thesis, Texas A&M University, TX.

Brandon, E.A.A., Davis, R.W., Kanatous, S., Calkins, D.G. & Loughlin, T.R. (1996) Pup condition and growth rates in declining and stable populations of Steller sea lions in Alaska. *Steller Sea Lion Recovery Investigations in Alaska, 1992–94*, pp. 62–68. Wildlife Technical Bulletin, 13. Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, AK.

Brekke, B. & Gabrielsen, G.W. (1994) Assimilation efficiency of adult kittiwakes and Brunnuck's guillemots fed capelin and Arctic cod. *Polar Biology*, **14**, 279–284.

Bulik, C.M., Sullivan, P.F., Fear, J.L., Pickering, A., Dawn, A. & McCullin, M. (1999) Fertility and reproduction in women with anorexia nervosa: a controlled study. *Journal of Clinical Psychiatry*, **60**, 130–135.

Calkins, D.G., Becker, E.F. & Pitcher, K.W. (1998) Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science*, **14**, 232–244.

Calkins, P. & Goodwin, E. (1988) *Investigation of the Declining Sea Lion Population in the Gulf of Alaska*, p. 76. Alaska Department of Fish and Game, Anchorage, AK.

Calkins, D.G., McAllister, D.C. & Pitcher, K.W. (1999) Steller sea lions status and trend in Southeast Alaska: 1979–1997. *Marine Mammal Science*, **15**, 462–477.

Calkins, D.G., Pendleton, G.W. & Pitcher, K.W. (1996) Steller sea lion population composition in a declining versus an increasing population. *Steller Sea Lion Recovery Investigations in Alaska, 1992–94*, pp. 19–24. Wildlife Technical Bulletin, 13. Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, AK.

Calkins, D.G. & Pitcher, K.W. (1982) *Population Assessment, Ecology, and Trophic Relationships of Steller Sea Lions in the Gulf of Alaska*, p. 546. Alaska Department of Fish and Game, Anchorage, AK.

Castellini, M.A. & Calkins, D.G. (1993) Mass estimates using body morphology in Steller sea lions. *Marine Mammal Science*, **9**, 48–54.

Castellini, M.A. & Costa, D.P. (1990) Relationships between plasma ketones and fasting duration in neonatal elephant seals. *American Journal of Physiology*, **259**, R1086–R1089.

Castellini, M.A., Davis, R.W., Loughlin, T.R. & Williams, T.M. (1993) Blood chemistries and body condition of Steller sea lion pups at Marmot Island, Alaska. *Marine Mammal Science*, **9**, 202–208.

Cherel, Y., Heitz, A., Calgari, C., Robin, J.-P. & Le Maho, Y. (1992) Relationships between lipid availability and protein utilization during prolonged fasting. *Journal of Comparative Physiology B*, **162**, 305–313.

Colares, E.P., Colares, I.G., Bianchini, A. & Santos, E.A. (2000) Seasonal variations in blood parameters of the Amazonian manatee, *Trichechus inunguis*. *Brazilian Archives of Biology and Technology*, **43**, 165–171.

Costley, G.E. (1970) Involvement of formaldehyde in depressed iron absorption in mink and rats fed Pacific hake (*Merluccius productus*). PhD Thesis, Oregon State University, OR.

Davis, R.W., Brandon, E.A.A., Adams, T.C.W.I., Iliams, T.M., Castellini, M.A., Loughlin, T.R. & Calkins, D.G. (1996a) *Indices of Reproductive Effort, Body Condition and Pup Growth for Steller Sea Lions (Eumetopias jubatus) in Alaska*, pp. 53–61. Alaska Department of Fish and Game, Anchorage, AK.

Davis, R.W., Brandon, E.A.A., Adams, T.C., Williams, T.M., Castellini, M.A., Loughlin, T.R. & Calkins, D.G. (1996b) Indices of reproductive effort, body condition and pup growth for Steller sea lions (*Eumetopias jubatus*) in Alaska. *Steller Sea Lion Recovery Investigations in Alaska, 1992–94*, pp. 53–61. Alaska Department of Fish and Game, Division of Wildlife Conservation, Wildlife Technical Bulletin 13, Anchorage, AK.

DeLong, R.L. & Antonelis, G.A. (1991) Impact of the 1982–1983 El Niño on the northern fur seal population at San Miguel Island, California. In: *Pinnipeds and El Niño: Responses to Environmental Stress* (Ed. by F. Trillmich & K. Ono), pp. 75–83. Springer-Verlag, New York.

DeMaster, D. & Atkinson, S. (2002) *Steller Sea Lion Decline: Is it Food II*, p. 80. University of Alaska Sea Grant, AK–SG–02–02, Fairbanks, AK.

Donnelly, C.P., Kitts, D.D. & Trites, A.W. (2003) Possible effects of pollock and herring on the growth and reproductive success of Steller sea lions: insights from feeding experiments using an alternative animal model. *Rattus Norvegicus. British Journal of Nutrition*, **89**, 71–82.

Ferrero, R.C., DeMaster, D.P., Hill, P.S., Muto, M.M. & Lopez, A.L. (2000) *Alaska Marine Mammal Stock Assessments*, p. 200. US Department of Commerce, NOAA, NMFS, AFSC, AK.

Frisch, R.E., Wyshak, G. & Vincent, L. (1980) Delayed menarche and amenorrhea in ballet dancers. *New England Journal of Medicine*, **303**, 17–19.

Fritz, L.W., Ferrero, R.C. & Berg, R.J. (1995) The threatened status of Steller sea lions, *Eumetopias jubatus*, under the Endangered Species Act: effects on Alaska groundfish fisheries management. *Marine Fisheries Review*, **57**, 14–27.

Geraci, J.R. (1975) Pinniped nutrition. *Rapports et Proces-Verbaux Des Reunion Conseil International Pour l'Exploration de la Mer*, **165**, 312–323.

Gerber, L.R. & Hilborn, R. (2001) Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review*, **31**, 131–150.

Grenfell, B. & Gulland, F.M.D. (1996) Introduction: ecological impact of parasitism on wildlife host populations. *Parasitology*, **111**, S3–S14.

Guinet, C., Jouventin, P. & Weimerskirch, H. (1999) Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease? *Antarctic Science*, **11**, 193–197.

Guinet, C., Roux, J.P., Bonnet, M. & Mison, V. (1998) Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology*, **76**, 1418–1424.

Gulich, M.P., Onoprienko, E.N. & Sokolova, A.G. (1990) Modified Alaska pollock protein hygenic evaluation based on pathomorphologic investigations. *Voprosy Pitaniia*, **3**, 39–43.

Harris, R.B.S. (1991) Growth measurements in Sprague-Dawley rats fed diets of very low fat concentration. *Journal of Nutrition*, **121**, 1075–1080.

Haug, T., Krøyer, A.B., Nilssen, K.T., Ugland, K.I. & Aspholm, P.E. (1991) Harp seal (*Phoca groenlandica*) invasions in Norwegian coastal waters: age composition and feeding habits. *ICES Journal of Marine Science*, **48**, 363–371.

Heath, C.B., Ono, K.A., Boness, D.J. & Francis, J.M. (1991) The influence of El Niño on female attendance patterns in the California sea lion. In: *Pinnipeds and El Niño: Responses to Environmental Stress*, **Vol. 88**. *Ecological Studies* (Ed. by F. Trillmich & K. A. Ono), pp. 138–145. Springer-Verlag, Berlin.

Hubbard, R.C. (1968) Husbandry and laboratory care of pinnipeds. In: *The Behavior and Physiology of Pinnipeds* (Ed. by R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice & R.J. Schusterman), pp. 299–358. Appleton-Century-Crofts, New York, NY.

Keyes, M.C. (1965) Pathology of the northern fur seal. *Journal of the American Veterinary Medical Association*, **147**, 1090–1095.

Kirsch, P.E., Iverson, S.J. & Bowen, W.D. (2000) Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). *Physiological and Biochemical Zoology*, **73**, 45–49.

Kjelliqwist, S.A., Huag, T. & Øritsland, T. (1995) Trends in age-composition, growth and reproductive parameters of Barents Sea harp seals, *Phoca groenlandica*. *ICES Journal of Marine Science*, **52**, 197–208.

Knox, G.A. (1994) *The Biology of the Southern Ocean*. Cambridge University Press, Cambridge.

Lawson, J.W., Hare, J.A., Noseworthy, E. & Friel, J.K. (1997a) Assimilation efficiency of captive ringed seals (*Phoca hispida*) fed different diets. *Polar Biology*, **18**, 107–111.

Lawson, J.W., Miller, E.H. & Noseworthy, E. (1997b) Variation in assimilation efficiency and digestive efficiency of captive harp seals (*Phoca groenlandica*) on different diets. *Canadian Journal of Zoology*, **75**, 1285–1291.

Loughlin, T.R. (1998) The Steller sea lion: a declining species. *Biosphere Conservation*, **1**, 91–98.

Lowry, L.F., Frost, K.J. & Loughlin, T.R. (1988) Importance of walleye pollock in the diets of marine mammals in the Gulf of Alaska and Bering Sea, and implications for fishery management. *Proceedings of the International Symposium of the Biology and Management of Walleye Pollock*, pp. 701–726. Anchorage, AK.

Lunn, N.J. & Boyd, I.L. (1993) Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. *Symposia of the Zoological Society of London*, **66**, 115–129.

Lunn, N.J., Boyd, I.L. & Croxall, J.P. (1994) Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology*, **63**, 827–840.

Mair, H. (1998) Sea lion populations take a pounding. *Marine Pollution Bulletin*, **36**, 116–117.

Majluf, P. (1991) El Niño effects on pinnipeds in Peru. In: *Pinnipeds and El Niño: Responses to Environmental Stress*, **Vol. 88**. *Ecological Studies* (Ed. by F. Trillmich & K.A. Ono), pp. 55–65. Springer-Verlag, Berlin.

Markussen, N.H. (1995) Changes in metabolic rate and body composition during starvation and semistarvation in harbour seals. In: *Developments in Marine Biology 4: Whales, Seals, Fish and Man* (Ed. by A.S. Blix, L. Walløe & Ø. Ulltang), pp. 383–391. Elsevier, Amsterdam.

Mathiak, K., Gowin, W., Hebebrand, J., Ziegler, A., Blum, W.F., Felsenberg, D., Lubbert, H. & Kopp, W. (1999) Serum leptin levels, body fat deposition, and weight in females with anorexia nervosa. *Hormone and Metabolic Research*, **31**, 274–277.

Matkin, C.G., Barrett-Lennard, L. & Ellis, G. (2002) Killer whales and predation on Steller sea lions. In: *Steller Sea Lion Decline: Is it Food II* (Ed. by D. DeMaster & S. Atkinson), pp. 61–66. University of Alaska Sea Grant, AK-SG-02–02, Fairbanks, AK.

McCafferty, D.J., Boyd, I.L., Walker, T.R. & Taylor, R.I. (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Marine Ecology Progress Series*, **166**, 285–299.

McShane, T.M. & Wise, P.M. (1996) Life-long moderate caloric restriction prolongs reproductive life span in rats without interrupting estrous cyclicity: effects on the gonadotropin-releasing hormone/luteinizing hormone axis. *Biology of Reproduction*, **54**, 70–75.

Merrick, R. (1995) The relationship of the foraging ecology of Steller sea lions (*Eumetopias jubatus*) to their population decline in Alaska. PhD Thesis, University of Washington, WA.

Merrick, R.L., Brown, R., Calkins, D.G. & Loughlin, T.R. (1995) A comparison of Steller sea lion, *Eumetopias jubatus,* pup masses between rookeries with increasing and decreasing populations. *Fishery Bulletin*, **93**, 738–758.

Merrick, R.L., Chumbley, M.K. & Byrd, G.V. (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1342–1348.

Merrick, R.L. & Loughlin, T.R. (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan Waters. *Canadian Journal of Zoology*, **75**, 776–786.

Merrick, R.L., Loughlin, T.R. & Calkins, D.G. (1987) Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956–86. *Fishery Bulletin*, **85**, 351–365.

Milette, L.L. (1999) Behaviour of lactating Steller sea lions (*Eumetopias Jubatus*) during the breeding season: a comparison between a declining and stable population in Alaska. MSc Thesis. University of British Columbia, Vancouver, BC.

Milette, L.L. & Trites, A.W. (in press) Maternal attendance patterns of lactating Steller sea lions (*Eumetopias jubatus*) from a stable and a declining population in Alaska. *Canadian Journal of Zoology*.

Miller, L.K. (1978) *Energetics of the Northern Fur Seal in Relation to Climate and Food Resources of the Bering Sea*, p. 26. Institute of Arctic Biology, Fairbanks, AK.

Nieuwenhuizen, A.G., Schuiling, G.A., Seijsener, F.J., Moes, H. & Koiter, T.R. (1999) Effects of food restriction on glucose tolerance, insulin secretion, and islet-cell proliferation in pregnant rats. *Physiology and Behavior*, **65**, 167–677.

Nillsen, K.T., Huag, T., Øritsland, T., Lindbolm, L. & Kjelliqwist, S.A. (1998) Invasion of harp seals *Phoca groenlandica* Erxleben to coastal waters of Norway in 1995: ecological and demographic implications. *Sarsia*, **83**, 337–345.

NMFS (National Marine Fisheries Service) (1992) *Recovery Plan for the Steller Sea Lion (Eumetopias jubatus)*. Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service, Silver Spring, MD.

NMFS (National Marine Fisheries Service) (2001) *Endangered Species Act. Section 7 Consultation – Biological opinion on authorization of Gulf of Alaska and Bering Sea/Aleutian Islands groundfish fisheries based on the Fishery Management Plan for the Gulf of Alaska and Bering Sea/Aleutian Islands groundfish as modified by amendments 61 and 70.* NMFS – Alaska Region, Protected Resources Division, Silver Spring, MD.

Nordøy, E.S. & Blix, A.S. (1991) Glucose and ketone body turnover in fasting grey seal pups. *Acta Physiologica Scandinavica*, **141**, 565–571.

Nordøy, E.S., Ingebretsen, O.C. & Blix, A.S. (1990) Depressed metabolism and low protein catabolism in fasting grey seal pups. *Acta Physiologica Scandinavica*, **139**, 316–369.

Olesiuk, P.F., Bigg, M.A. & Ellis, G.M. (1990) Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 992–1003.

Ono, K.A., Boness, D.J. & Oftedal, O.T. (1987) The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behavioral Ecology and Sociobiology*, **21**, 109–118.

Øritsland, T. (1990) Seals in the northeast Atlantic and interactions with fisheries. *Comité Arctique International Commentary*, **2**, 10–13.

Øritsland, N.A. & Markussen, N.H. (1990) Outline of a physiologically based model for population energetics. *Ecological Modelling*, **52**, 267–288.

Peckham, S.C., Entenman, C. & Carroll, H.W. (1962) The influence of a hypercaloric diet on gross body and adipose tissue composition in the rat. *Journal of Nutrition*, **77**, 187–197.

Perez, M.A. (1994) *Calorimetry Measurements of Energy Value of some Alaskan Fishes and Squids*, **Vol. 32**, p. 32. US Department of Commerce, NOAA Technical Memoir, NMFS-AFSC.

Pitcher, K.W. (1990) Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science*, **6**, 121–134.

Pitcher, K.W. (2002) Nutritional limitation? An alternative hypothesis. In: *Steller Sea Lion Decline: Is it Food II* (Ed. by D. DeMaster & S. Atkinson), pp. 15–18. University of Alaska Sea Grant, AK-SG-02–02, Fairbanks, AK.

Pitcher, K.W., Calkins, D.G. & Pendleton, G.W. (1998) Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? *Canadian Journal of Zoology*, **76**, 2075–2083.

Pomeroy, P. & Duck, C. (2000) Breeding performance of grey seals at the Isle of May. In: *The Effect of Large-Scale Industrial Fisheries on Non-Target Species* (Ed. by J. Harwood). Final Report to DGXIV, Directorate General Fisheries of the European Commission, under Contract 95/78.

Porter, B. (1997) Winter ecology of Steller sea lions (*Eumetopias jubatus*) in Alaska. MSc Thesis, University of British Columbia, Vancouver, BC.

Privett, O.S., Pusch, F.J., Holman, R.T. & Lundberg, W.O. (1960) Essential fatty acid properties of tuna, herring and menhaden oils. *Journal of Nutrition*, **71**, 66–69.

Raum-Suryan, K.L., Pitcher, K.W., Calkins, D.G., Sease, J.L. & Loughlin, T.R. (2002) Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. *Marine Mammal Science*, **18**, 746–764.

Rea, L. (1995) Prolonged fasting in pinnipeds. PhD Thesis, University of Alaska Fairbanks, Fairbanks, AK.

Rea, L.D., Castellini, M.A., Fadely, B.S. & Loughlin, T.R. (1998) Health status of young Alaska Steller sea lion pups (*Eumetopias jubatus*) as indicated by blood chemistry and hematology. *Comparative Biochemistry and Physiology Part A*, **120**, 617–623.

Rea, L.D., Rosen, D.A.S. & Trites, A.W. (2000) Metabolic response to fasting in 6-week-old Steller sea lion pups (*Eumetopias jubatus*). *Canadian Journal of Zoology*, **78**, 890–894.

Rosen, D.A.S. & Trites, A.W. (1997) Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. *Comparative Biochemistry and Physiology*, **118A**, 877–881.

Rosen, D.A.S. & Trites, A.W. (1999) Metabolic effects of low-energy diet on Steller sea lions, *Eumetopias jubatus*. *Physiological and Biochemical Zoology*, **72**, 723–731.

Rosen, D.A.S. & Trites, A.W. (2000a) Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon. *Canadian Journal of Zoology*, **78**, 1–6.

Rosen, D.A.S. & Trites, A.W. (2000b) Pollock and the decline of Steller sea lions: testing the junk food hypothesis. *Canadian Journal of Zoology*, **78**, 1243–1250.

Rosen, D.A.S. & Trites, A.W. (2002) What is it about food? Examining possible mechanisms with captive Steller sea lions. In: *Steller Sea Lion Decline: Is it Food II* (Ed. by D. DeMaster & S. Atkinson), pp. 45–48. University of Alaska Sea Grant, AK-SG-02–02, Fairbanks, AK.

Rouvinen, K.I., Anderson, D.M. & Alward, S.R. (1997) Effects of high dietary levels of silver hake and Atlantic herring on growing-furring performance and blood clinical-chemistry of mink (*Mustela vison*). *Canadian Journal of Animal Science*, **77**, 509–517.

Roux, J.-P. (1997) *Proceedings of the International Workshop on Research and Management of Cape Fur Seals in Namibia*, p. 60. Ministry of Fisheries and Marine Resources of Namibia, Swakopmund, Namibia, 24–26 June 1997.

Scheffer, V.B. (1950) Winter injury to young fur seals on the northwest coast. *California Fish and Game*, **34**, 278–279.

Sease, J.L. & Loughlin, T.R. (1999) *Aerial and Land-Based Surveys of Steller Sea Lions (Eumetopias Jubatus) in Alaska, June and July 1997 and 1998*, p. 61. US Department of Commerce. NOAA Technical Memoir, NMFS-AFSC-100, Seattle, WA.

Sease, J.L. & Merrick, R.L. (1997) Status and population trends of Steller sea lions. In: *Pinniped Populations, Eastern North Pacific: Status, Trends and Issues; A Symposium of the 127th Annual Meeting of the American Fisheries Society* (Ed. by G. Stone, J. Goebel & S. Webster), pp. 22–30. New England Aquarium and Monterey Bay Aquarium, Monterey, CA.

Sinclair, E.H. & Zeppelin, T.K. (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy*, **83**, 973–990.

Stansby, M.E. (1969) Nutritional properties of fish oils. *World Review of Nutrition and Dietetics*, **11**, 46–105.

Stansby, M.E. (1976) Chemical characteristics of fish caught in the northeast Pacific Ocean. *Marine Fisheries Review*, **38**, 1–11.

Stout, F.M., Oldfield, J.E. & Adair, J. (1960) Nature and cause of the 'cotton-fur' abnormality in mink. *Journal of Nutrition*, **70**, 421–426.

Thomas, G.L. & Thorne, R.E. (2001) Night-time predation by Steller sea lions. *Nature*, **411**, 1013–1013.

Thompson, P.M., Corpe, H.M. & Reid, R.J. (1998) Prevalence and intensity of the ectoparasite *Echinophthirius horridus* on harbour seals (*Phoca vitulina*): effects of host age and inter-annual variability in host food availability. *Parasitology*, **117**, 393–403.

Thompson, P.M., Tollit, D.J., Corpe, H.M., Reid, R.J. & Ross, H.M. (1997) Changes in haematological parameters in relation to prey switching in a wild population of harbour seals. *Functional Ecology*, **11**, 743–750.

Trillmich, F. (1986) Attendance behavior of Galapagos fur seals. In: *Fur Seals: Maternal Strategies on Land and at Sea* (Ed. by R.L. Gentry & G.L. Kooyman), pp. 168–185. Princeton University Press, Princeton, NJ.

Trillmich, F. (1990) The behavioral ecology of maternal effort in fur seals and sea lions. *Behavior*, **114**, 3–20.

Trillmich, F. & Dellinger, T. (1991) The effects of El Niño on Galapagos pinnipeds. In: *Pinnipeds and El Niño: Responses to Environmental Stress. Ecological Studies* (Ed. by F. Trillmich & K.A. Ono). Springer-Verlag, Berlin.

Trillmich, F. & Limberger, D. (1985) Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia*, **67**, 19–22.

Trites, A.W. (1991) Fetal growth of northern fur seals: life history strategy and sources of variation. *Canadian Journal of Zoology*, **69**, 2608–2617.

Trites, A.W. (1992) Northern fur seals: why have they declined? *Aquatic Mammals*, **18**, 3–18.

Trites, A.W. & Larkin, P.A. (1996) Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? *Aquatic Mammals*, **22**, 153–166.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A.M. & Pauly, D. (1999) *Ecosystem Change and the Decline of Marine Mammals in the Eastern Bering Sea: Testing the Ecosystem Shift and Commercial Whaling Hypotheses*, p. 106. Fisheries Center, UBC, Vancouver, Canada.

Trites, A.W. & Porter, B.T. (2002) Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. *Journal of Zoology*, **256**, 547–556.

Trites, A.W., Porter, B.P., Deecke, V. & Rosen, D.A.S. (2001) Observations of Steller sea lions at haulouts in Alaska: when do they wean and are they nutritionally stressed? [abstract]. *14th Biennial Conference on the Biology of Marine Mammals*, Vancouver, British Columbia, Canada.

Walford, L.A. & Wilber, C.G. (1955) The sea as a potential source of protein food. *Advances in Protein Chemistry*, **10**, 289–316.

Westerterp, K.R., Donkers, J.H.H.L.M., Fredrix, E.W.H.M. & Boekhoudt, P. (1995) Energy intake, physical activity and body weight: a simulation model. *British Journal of Nutrition*, **73**, 337–347.

Winship, A. & Trites, A.W. (2003) Prey consumption by Steller sea lions in Alaska: How much do they require? *Fishery Bulletin*, **101**, 147–163.

Winship, A.J., Trites, A.W. & Calkins, D.G. (2001) Growth in body size of the Steller sea lion. *Journal of Mammalogy*, **82**, 500–519.

Winship, A.J., Trites, A.W. & Rosen, D.A.S. (2002) A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska. *Marine Ecology Progress Series*, **229**, 291–312.

York, A.E. (1994) The population dynamics of northern sea lions, 1975–1985. *Marine Mammal Science*, **10**, 38–51.

Zagzebski, K.A., Phillips, A.V. & Gulland, F.M.D. (1999) The impact of the 1998 El Niño on pinniped strandings in central California, [abstract]. *13th Biennial Conference on the Biology of Marine Mammals*, p. 208. Maui, HI.

Zenteno-Savin, T., Castellini, M., Rea, L.D. & Fadely, B.S. (1997) Plasma haptoglobin levels in threatened Alaskan pinniped populations. *Journal of Wildlife Diseases*, **33**, 64–71.

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